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LOCAL DISTRIBUTION OF GRASSHOPPERS IN RELATION TO PLANT ASSOCIATIONS.

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CONTENTS.

I. INTRODUCTION.

During the summer of 1912, while at the biological station of the University of Michigan, at Douglas Lake, the writer found opportunity to study the relation between local distribution of grasshoppers and the plant associations. The group studied includes the three subfamilies *Tryxalinæ*, *Œdipodinæ*, and *Acridiinæ*, of the orthopteran family *Acrididæ*.

Habitat-distribution of *Orthoptera* has received considerable attention. Published accounts of *Orthoptera* contain the bulk of the data on habitats. The studies of Morse ('04), and of

Hancock ('11), classifying these insects on the basis of habitat, have been reviewed by Shelford ('12*b*: 352). Biological surveys of certain regions, as the Michigan surveys, have included local distribution of grasshoppers (Adams, '06, '08; Ruthven, '11; Hart and Gleason, '07). Studies of animal communities have included data on grasshopper distribution (Shelford, '12*a*; Vestal, '13*b*). In these two studies not all of the associations of the region were considered. In many of the above accounts the concept of the plant association as a habitat has appeared incidentally or not at all; this concept was used in a study of local distribution of birds, by Gates ('11). In the present study all the plant associations of the region have been included, and the plant association has been used as the index of the habitat. In general the results indicate that the important factors of local distribution are, in initial stages of development of the vegetation, *physical* conditions of the environment; in advanced stages, *vegetational* conditions; in either case, the character of the plant association is the index to local environmental conditions for grasshoppers. Collection data are in another paper (Vestal, '13*a*).

Physiography of the Region.

Douglas Lake is situated less than twenty miles south of the northern tip of the southern peninsula of Michigan, in Cheboygan county. There are two main physiographic types, the first being old beaches and lake bottoms of the Nippissing and Algonquin Lakes, and the second morainic in origin. The soil of the first type is almost pure sand; the relief is very slight. The morainic lands have typical rolling topography; they are of mixed composition, usually with loam or sandy loam surface soil. Streams are small and few, but on the whole the region is well drained, the soil being porous. Swamps occupy a very small proportion of the area, and are usually drained. Undrained swamps are few and small in the immediate vicinity.

The lake is about four miles long, with irregular contour, and lies north of a chain of lakes which in recent geological time connected Lakes Michigan and Huron. Douglas Lake was itself, previous to this time, a part of the connection. Much of the shore line is sandy beach, with occasional sand-bars and spits,

and in several places lagoons. Wave action is considerable on exposed parts of the shore-line, but the exposed sand has been very little acted upon by wind. Beach dunes occur sparingly and are of small area.

General Character of the Vegetation.

Much of this part of Michigan is covered with two general types of vegetation, which give rise to the common terms "pine lands" and "hardwood lands." The pine forests have been developed on the more sandy areas, the hardwoods on the loamy or clay moraines. "Hardwood lands" are of much greater agricultural value, and the more extensive farming districts are in morainic regions. The pine lands have been largely deforested, and fire has also been very prevalent, so that many of the original pine forests have been replaced by growths of the large-toothed aspen. In the immediate region of the biological station virtually no pine forest remains, though scattering growths of pitch pine are not rare along the beach, and a few pines are to be found scattered among the aspens. The aspen forest occupies more than one half of the entire area studied; the hardwood forest and hardwood clearings somewhat more than a fourth of the area, and other kinds of vegetation considerably less than one fourth. These other kinds of vegetation are grassland areas, cultivated fields, meadows and sedge growths, cedar bogs, and open peat bogs. The plant associations have been studied in detail by Gates ('13), with reference to a much larger area than has been covered in the present study.

II. The Plant Associations and the Grasshoppers which Occur within Them.

Associations of two vegetation regions or *vegetation provinces* (Gleason, '10: 42–45) occur within the area. The coniferous forests, the aspen forests, heaths and bogs of the region, typical of the northeastern states and much of Canada, represent the *Northeastern Conifer Province.* The deciduous forest (hardwoods) and the herbaceous and thicket growths of hardwood clearings represent the *Eastern Deciduous Forest Province.* While primarily consisting of these two geographic elements, the vegetation also includes *local associations*, particularly those

determined by local conditions of moisture; these are usually not characteristic of any one vegetation province; and *ruderal associations*, composed of introduced plants. Plant names used are those of Gray's Manual, seventh edition.

Associations of the Northeastern Conifer Province.

The culminating type of vegetation in the Northeastern Province is the balsam-spruce-birch forest, which is developed successively through lichen, heath, and different pine stages, in xerophytic situations; and through bog and bog-forest stages in water and wet ground. Only those associations are listed which are represented by distinct areas in the region studied.

Chamædaphne Association (Gates, '13: 57).—No grasshoppers were taken in the open bogs of cassandra. In Ontonagon county, northern Michigan, thickets of cassandra, alder, wax myrtle, high-bush cranberry, etc., are the habitat for *Podisma glacialis* and *Melanoplus islandicus* (Morse, '06: 70).

Thuja Association (Gates, '13: 66).—The cedar or arbor-vitæ growth known as Rees's bog, near the shore of Burt Lake, south of Douglas Lake, was studied. In this bog the peat soil is less than two feet deep, the substratum being sand or gravel. It is drained through the porous soil into Burt Lake. No bare soil is exposed, but partly moss-grown logs lying upon the surface are not infrequent. Trees are usually not more than twenty feet in height, but are close together, and cast a deep shade. *Thuja occidentalis* is the dominant species; *Larix laricina*, tamarack, and *Picea mariana*, black spruce, occur sparingly. The surface is a thick carpet of *Sphagnum;* many peat-bog plants, as *Cornus canadensis*, orchids, ericads, etc., are present, more abundantly in less shaded parts. The only grasshopper species taken in this bog is *Melanoplus islandicus*.

Aspen Association (Gates, '13: 77).—The extensive sandy pine lands of the region are now, as a result of fires and cutting, practically all occupied by the aspen forest. The dominant tree is the large-toothed aspen, *Populus grandidentata*. Other frequent species are paper birch, beech, red oak, hard maple, red maple, wild cherry, *Prunus pennsylvanica*, white pine, pitch pine. The undergrowth, quite similar to that of the pine forest, is chiefly composed of bushy blueberry plants, *Vaccinium penn-*

sylvanicum, which are close together and usually less than six inches high, and of the taller and less numerous plants of the bracken fern, *Pteris aquilina*. Other plants are the bush honeysuckle, *Diervilla lonicera*, and several grasses and composites. Near the lake beach patches of bearberry, *Arctostaphylos uva-ursi*, and of dwarf juniper, *Juniperus horizontalis*, form small heaths. Over all the open aspen growth, a considerable proportion of bare sandy soil is exposed, in the interspaces between plants. Dead leaves, partly decayed and partly burned stumps and logs, litter the surface. There are a number of bare roadways.

The tree growth is irregular, being entirely absent in frequent local areas which vary in size from small unshaded patches between trees to areas thirty meters in diameter. In such places there are indications that the undergrowth is practically independent of the trees. In the older tree growths the hardwood species have assumed control, indicating development into hardwood forest. Ground conditions are more like those of closed forest.

In the treeless parts of the association, in the bracken-blueberry growth, *Melanoplus angustipennis* is the common grasshopper species. *Melanoplus atlanis* and *Camnula pelludica* are common, and *M. bivittatus* occasional, along roadways. *M. luridus* is found sparingly in scattered aspen growths. *Scirtetica marmorata* occurs usually on or near the lichen-covered surfaces. *M. fasciatus* is more often found in the closed forest. On the sandy roads, and sparingly in the sandy interspaces between the plants, are found *M. atlanis*, *M. angustipennis*, *Dissosteira carolina*, *Spharagemon bolli*, *Circotettix verruculatus*, *Arphia pseudonietana*, *Hippiscus tuberculatus*.

Associations of the Eastern Deciduous Forest Province.

The most highly developed form of deciduous forest vegetation is the beech-maple or beech forest, well represented in the region. This develops, on dry soil, through herbaceous, thicket, and xerophytic oak stages, usually, followed by mesophytic red oak and maple stages. The following associations were studied in the Douglas Lake region:

Herbaceous Associations (Gates, '13: 75).—The common fireweed, *Epilobium angustifolium*, is the first plant to establish itself

on newly cleared or burned hardwood land. The clearings are soon overgrown with herbaceous plants, many of them introduced, as mullein, *Verbascum thapsus*. These burns and clearings vary considerably both as regards physical conditions and plant composition. They are only temporary stages in the process of reforestation. Usually they are dry and hot, being fully exposed to the sun, but often sheltered from wind by surrounding forests. Grasshoppers are numerous, both in individuals and in species. In approximate order of abundance they are: *Melanoplus atlanis*, *Camnula pellucida*, *Dissosteira carolina*, *M. bivittatus*, *Spharagemon bolli*, *Circotettix verruculatus*, *M. luridus*, *Chloealtis conspersa*, *M. minor*. Only the first two occur in any considerable abundance.

Thicket and Bramble Associations (Gates, '13: 76).—The shrubby plants which replace the herbs in clearings are principally blackberry and raspberry, *Rubus* spp., red-berried elder, *Sambucus racemosa*, and young seedlings and shrubs of hard maple, *Acer saccharum*. These growths often form a dense tangle which is almost impenetrable. In dense parts of these thickets an occasional *Melanoplus bivittatus* would be seen upon a leaf at the top of a shrub. Where the ground could be seen, *Melanoplus atlanis*, *Camnula pellucida*, and *Chloealtis conspersa* were also to be found.

Beech-Maple Association (Gates, '13: 71).—The beech-maple forest is dominated by two tree species, *Fagus grandifolia*, which occurs in places in nearly pure stands, and *Acer saccharum*. *Tsuga canadensis*, the hemlock, is also important in places. *Ostrya virginiana*, *Betula lutea*, and *Tilia americana* are infrequent species. In the deeply shaded parts of the forest, the undergrowth consists mainly of young seedlings of *Fagus* and *Acer*, with small plants of *Maianthemum canadense* and *Mitchella repens*, partly hidden in the thick carpet of fallen leaves. In the sunlit spots the undergrowth is taller, with *Acer pennsylvanicum* and *Sambucus racemosa*. Many other forest plants occur. Stumps and logs are common, but no bare ground is exposed. The relative humidity is high. Exposure to sun and wind is at a minimum. *Melanoplus islandicus* is a characteristic grasshopper species, of the deeply shaded parts of the forest. It is probable that *Podisma glacialis variegata* occurs also on shrub-

bery. In more open parts of the hardwood forest, and near the edges of clearings, most of the grasshopper species that are common in clearings were also found, in very small numbers, however.

Ravine Forest Association (Gates, '13: 66–70).—This association is best developed in the ravine occupied by what is locally known as *Big Springs*. A number of springs, fed by the underground drainage from Douglas Lake, to the north, form the head of Carp Creek, which runs south to Burt Lake. The ground is very wet, and is occupied by bog plants and deciduous forest undergrowth. Trees are *Tilia americana*, *Tsuga canadensis*, *Fagus grandifolia*, *Ostrya virginiana*, *Betula lutea*, *Acer saccharum*, *Abies balsamea*. Succession has proceeded from the coniferous bog forest toward the beech-maple association. *Podisma glacialis variegata*, recorded from Carp Creek, probably was taken in this ravine forest, *Melanoplus islandicus* probably also occurs in the same association.

Local Associations.

Dry Beach Associations (Gates, '13: 55).—Quite a number of the strand plants of the sandy margins of Douglas Lake belong to an assemblage which is characteristic of the sand shores of the Great Lakes. Three of these independently form associations in the region. These are *Elymus canadensis*, *Ammophila arenaria*, and *Potentilla anserina*. *Elymus* forms a low, narrow dune about one eighth mile long, at the southeastern end of the lake. It and *Ammophila* are found just above the level of wave action at many places on the shore. Sandbars on the north shore were partly covered by *Potentilla* growth. In these beach associations the soil is pure sand, dry and shifting, with full exposure to sun and wind. The vegetation is dry and scanty. Grasshoppers typical of these situations are: *Melanoplus atlanis*, *M. angustipennis*, *M. bivittatus*, *Camnula pellucida*, and *Dissosteira carolina*. Two species not taken at Douglas Lake, *Spharagemon wyomingianum* (Thomas), and *Trimerotropis maritima* (Harris), are very characteristic of beaches and dunes of the Great Lakes; both are recorded by Shull from the Saginaw Bay region ('11: 225–226).

Marsh Associations (Gates, '13).—Communities of marsh

plants bordering lakes, streams, and certain open bogs are usually composed of only one or a few plant species. These growths, depending upon local conditions of moisture, are frequently small in area, and different stations are not always alike. Conditions of shade and of soil are variable. No grasshoppers were found upon the marsh plants which grew standing in open water, although in dense growths individuals sometimes stray beyond the shore. The numbers of grasshoppers vary considerably in different stations. They are most numerous in tall, rather close, sedge or grass growths. *Stenobothrus curtipennis* is the characteristic grasshopper of littoral situations. *Melanoplus atlanis*, *M. bivittatus*, and *M. differentialis* are less frequently found. *M. femur-rubrum*, though not taken by the writer, is often found in such places. The *Melanopli* are more numerous in the higher and more open parts, while *Stenobothrus* occurs farthest out towards the water.

Ruderal Associations.

In the Douglas Lake region much of the native forest has been removed by cutting and burning, and its place has been taken by cultivated crops and weed growths. In addition many plant associations, though not destroyed, have been materially changed, and native animals have also been much affected. Secondary successions are principally due to interference by man. Most of the sandy land is now occupied by aspens as a result of destruction of the pines. One of the most important plants favored by artificial conditions is the blue-grass, *Poa pratensis*, which enters into nearly all ruderal growths. Other species of *Poa* probably occur in the region.

Ruderal Dry Grassland Associations.—Abandoned fields, dry pastures, roadside growths, and modified aspen undergrowth are the common forms of ruderal growth in dry situations. They are necessarily very different in physical conditions and plant composition, depending upon differences in original status and subsequent modification. In certain large areas west of Douglas Lake, near Pellston, a growth of bluegrass has almost entirely replaced the aspen association. Near the lake bluegrass invades the aspens along roadways, and one can trace long abandoned roads by the presence of this plant. Other weed species are

numerous. Grasshopper species of ruderal dry grassland are, in approximate descending order of importance: *Melanoplus atlanis*, *Camnula pelludica*, *M. bivittatus*, *Dissosteira carolina*, *Arphia pseudonietana*. All of these species, with the possible exception of the last, are more abundant in ruderal than in native vegetation.

Sparsely Vegetated or Bare Soil.—The condition of bare soil is much more frequent, in humid climates, as a result of disturbance. Plowed fields and constantly trampled paths and roads are the commonest areas of bare soil, and these furnish suitable habitats for those species which normally rest on bare soil, not on the plants. The *Œdipodinæ* are of this habit to a large extent. The character of the soil is important for oviposition, and though the bare soil grasshoppers are more or less migratory, certain of them are found associated with particular types of soil. Hart gives the soil-preferences for a number of the *Melanopli* in a sand region in Illinois ('07: 214, 215). It is to be remembered that bare soil as a habitat is not sufficient; nearby vegetation is necessary, and in this region is always present. Where extensive areas of bare soil occur, grasshoppers are very rare except at the border. The insects are conspicuous in bare places, as roads, but are more abundant in the interspaces between plants, in open growths. Areas of bare soil differ from the sparsely vegetated areas merely in degree, and are really the same kind of habitat. In the region studied considerable bare soil is exposed along the beach, but in the aspen association roads are the typical areas of bare and sparsely-grown soil, as also in the hardwood district. Interstitial grasshoppers which are conspicuous in bare soil are: *Dissosteira carolina*, *Arphia pseudonietana*, *Circotettix verruculatus*, *Spharagemon bolli*, and *Hippiscus tuberculatus*. Those of open grassland, frequently found on bare soil of interstices, and less frequently on bare soil of roads, are: *Camnula pellucida*, *Melanoplus atlanis*, *M. bivittatus*, *M. angustipennis*.

Meadow Associations.—Ruderal meadows and swales, like the native marsh and littoral associations, are variable in character. Probably the most common type is the bluegrass-white clover meadow. It is found in wet pastures and along boggy roads; it forms a very low, dense carpet, resembling a closely trimmed lawn, and probably always depends on constant cropping of

cattle. It is of common occurrence on the north shore of Douglas Lake, and near Munro Lake, several miles north. In this type of meadow *Melanoplus atlanis* and *Stenobothrus curtipennis* are of about equal abundance. *M. femur-rubrum* was not taken, but is more abundant in such places in other localities than is *M. atlanis*. *M. differentialis* is typical in meadow habitats, and *M. bivittatus* is found sparingly.

Arrangement of the Associations as Habitats.

The associations of any particular region may be placed in groups with respect to several well-known criteria. One of the prevalent methods is to consider together all associations which are genetically related, which form a developmental series, each stage being succeeded by the next in order, until the ultimate or climax association is reached. Another mode of classification is geographic, placing together all associations of like geographic distribution, all typical of a definite climatic region, an ecological province. Another grouping is based upon growth-form: by this treatment associations dominated by plants of similar growth-form, indicating physiological likeness, would be considered similar, regardless of geographic or successional relationships. The common division of associations of a region into climatic or geographic, and edaphic or local, is based upon local distribution or habitat. The grouping into aquatic and terrestrial is a grouping based upon habitat in a larger sense: the medium of life is the important feature. Finally it is necessary to distinguish between primary, original or native associations, and secondary, ruderal or cultural associations, wherever human influence has modified primeval conditions. These different groupings are not at all parallel, but form a complex. To orient an association with respect to others of the same region it is necessary to find its place in this complex. In a regional treatment it is usually necessary to consider all of these criteria. For different purposes, different bases of classification may be emphasized, but in no case should one basis be confused with another.

For the purpose of the present study, in which the plant associations are considered mainly as habitats for grasshoppers, two bases of classification receive emphasis. The first is with respect

to habitat, the second with respect to growth-form of the plants. These two considerations determine the physical and vegetational conditions to which the grasshopper species are subjected.

It is to be understood that grasshoppers are animals of the ground stratum and of the herbaceous stratum. In so far as these strata are similar as habitats in different plant associations, these associations may be treated together. Considerations as to whether associations are proximate or ultimate, geographic or local, native or ruderal, whether they belong to the Northeastern Province or the Deciduous Forest Province, are of interest only as they affect relative area of different associations within the region, and consequently the relative frequency and abundance of the grasshopper species of the different associations. In the following synopsis, the moisture factor is used for the division according to habitat, though other physical factors, such as soil, might have been used if it had been desirable to subdivide further. The synopsis arranges the associations of the region according to their similarity as habitats for grasshoppers.

Herbaceous or grassland associations.
- In wet or moist habitats.
  - Sedge and other littoral associations.
  - Meadow associations.
- In dry habitats.
  - Sparsely vegetated or bare soil.
  - Beach-grass associations.
  - Ruderal dry grassland.
  - Hardwood clearings.
  - Bracken-blueberry growth of open aspen forest.

Forest associations.
- In wet or moist habitats.
  - Cedar bog forest.
  - Ravine forest.
- In mesophytic habitats.
  - Closed aspen forest.
  - Beech-maple (hardwood) forest.

Among the dry grassland associations, variable conditions (resultants of both physical and vegetational agencies) are: texture and compactness of soil, humus content, proportion of bare surface; height, density, and general character of the vegetation. Sparsely vegetated grassland has a high proportion of bare surface; roadways and other small areas of bare soil are to be considered as part of an area of open vegetation.

It should be pointed out that conditions in the ground stratum of the aspen association are the same in the open treeless parts as among scattered trees. Exposure to sun and wind, as well as the vegetation, are almost identical in the two places. The open aspen forest is then, so far as its ground stratum is concerned, *a grassland association*. This is in accord with the results of Shelford ('12*a*: 82), who found that ground stratum conditions in open forests in sand at the lower end of Lake Michigan lag behind in the succession from herbaceous to forest growth. In reality open forests of very scattered trees are usually mixed associations, dominated in places by trees, and in more open places by herbaceous plants. So far as ground conditions are concerned, the association is herbaceous, and the bracken-blueberry growth is accordingly grouped with dry grassland. Ground conditions are not those of forest until the closed stage of the aspen association is reached. The lichen growth of open aspen areas, affording a locally different environment, may be regarded as a minor division of that association.

A primary division in the above synopsis, "shrub associations," might have been added. The thicket and bramble associations were small in area, were little studied, and as the conditions in the ground stratum in thickets are much the same as those in the hardwood forests, with about the same grasshopper assemblage, this division is omitted for simplification.

The grasshopper assemblages of these associations are presented in summarized form in the third section of this paper, which here follows.

III. Summary of Local Distribution of the Species.

The table which follows summarizes the habitat relations of the grasshopper species, and includes an approximate estimate of the numerical status of each species in each of its habitats. The method of numerical estimation is described on p. 165. It is necessary at this point to define the terms used to denote degrees of frequency, or regularity of occurrence, and abundance, or numbers of individuals per unit of area. *Dominant* species in a habitat, usually only one or two, have a very high abundance, and a high frequency, in that habitat. *Abundant* species are also

Table I.

Summarizing Habitat Relations of the Grasshoppers of the Douglas Lake Region.

Terms denoting degrees of frequency and abundance are defined immediately above, and are abbreviated in the table. Question-marks are inserted to indicate probable occurrence in habitats little studied. Where a space is blank it is understood that the species occurs accidentally or not at all in the particular habitat.

	Moist Grassland.		Dry Grassland.					Forest.			
	Sedge Growths.[2]	Wet Meadow.[2]	Bare Soil.[2]	Beach-grass.[2]	Ruderal Grass-land.[2]	Bracken-Blueberry.	Hard-wood Clearings.	Closed Aspens.	Beech-Maple.	Ravine Forest.	Thuja Bog.
Stenobothrus curtipennis (Harris)	Freq.	Freq.		Accid.							
Melanoplus differentialis (Thomas)		Freq.			Freq.	Occas.	?		?		
Melanoplus bivittatus (Say)		Freq.	Infreq.	Occas.	Freq.[1]	Occas.	Freq.		Infreq. or Accid.		
Melanoplus femur-rubrum (De Geer)		Freq.?		?	Freq.?	?	Freq.?				
Melanoplus atlanis (Riley)		Abund.	Freq.[1]	Abund.	Dom.	Freq.	Abund.	?	Infreq. or Accid.		
Camnula pellucida (Scudder)		Accid.	Freq.[1]	Freq.[1]	Dom.	Freq.[1]	Abund.	?	Infreq. or Accid.		
Melanoplus minor (Scudder)							Infreq. or Occas.				
Melanoplus luridus (Dodge)				?	?	Occas.	Occas.				
Melanoplus angustipennis (Dodge)			Occas.	Freq.	Infreq.	Dom.					
Dissosteira carolina (Linnæus)			Freq.[1]	Freq.	Freq.[1]	Occas.	Freq.[1]				
Spharagemon bolli Scudder			Freq.[1]	Occas.		Occas.	Occas.		Infreq. or Accid.		
Arphia pseudonietana (Thomas)			Freq.[1]	Infreq.	Freq.[1]	Infreq.	?				
Hippiscus tuberculatus (Palisot)			Freq.	Infreq.	?	Infreq.	?				
Circotettix verruculatus (Kirby)			Freq.	Occas.	Occas.	Occas.	Occas.		Infreq. or Accid.		
Scirtetica marmorata (Harris)						Infreq.[3]	?	?			
Melanoplus fasciatus (Barnston-Walker)						Infreq.	Infreq.[4]	Freq.[1]			
Chloealtis conspersa (Harris)						?	Occas.	Infreq. or Occas.	?		
Podisma glacialis variegata Scudder									?	Occas.?	?
Melanoplus islandicus Blatchley									Freq.	?	Occas.

[1] Frequently found, usually not in numbers, but in a few places approaching abundance.

[2] Stations representing these five habitats were rather variable as to physical and vegetational conditions, and also as to the numbers and species of the grasshoppers. Data for these five columns were compiled from more detailed tables in which a vertical column was assigned to each station of each of these habitats.

[3] More typical of the lichen-covered surface in more or less sheltered parts of the bracken-blueberry growth. In the association as a whole the species is infrequent; in lichen patches it is frequent.

[4] One specimen of the long-winged form, *M. f. volaticus*, was taken in the grassy border of a growth of hardwoods.

frequent; they are usually to be found in the habitat in considerable numbers at any time. *Frequent* refers to grasshoppers occurring regularly in the habitat, though not always to be found, and seldom numerous when found. *Occasional*, occasionally found in the habitat, not frequent or abundant. *Infrequent*, not often found in the habitat. *Accidental*, occurring in a habitat rare or unusual for the species. Specimens are usually found singly and the abnormal habitat frequently adjoins one in which the species is more regularly found.

The obvious facts shown by the table are:

1. Grasshoppers are more abundant, in species and in individuals, in herbaceous or grassland habitats than in forest, and more abundant in dry than in moist or wet situations.

2. Certain species are much more restricted than others in range of habitats, and in accompanying range of toleration of physical and vegetational factors of the environment.

3. Although a species may be found over several associations, it is more abundant in one, or two, of these, than in others (Certain activities take place in more restricted habitats; chief of these restricted activities is the laying of eggs.)

4. No two plant associations have identical grasshopper assemblages.

5. No two grasshopper species have identical habit-preferences.

These facts and others are considered in order in the general discussion.

In general, with every change of habitat there is a change in the assemblage of grasshopper species. These replace one another in the various habitats, often with considerable overlap, but all can be arranged with respect to gradients of environmental conditions. Gradients of several factors which vary together may in general be said to run parallel with the development of vegetation. This development of vegetation is in part the result, in part the cause, of these changes of physical and vegetational conditions.

The variation of environmental conditions can be expressed graphically by lines representing gradients of the factors which change with development of vegetation. Environmental conditions in each successional series may be represented by a line,

at one end of which the conditions are those of sterile soil or water, environmental control being entirely physical; at the other end conditions are those of the closed, completely developed, climatic association, vegetational control of local environment being nearly complete.

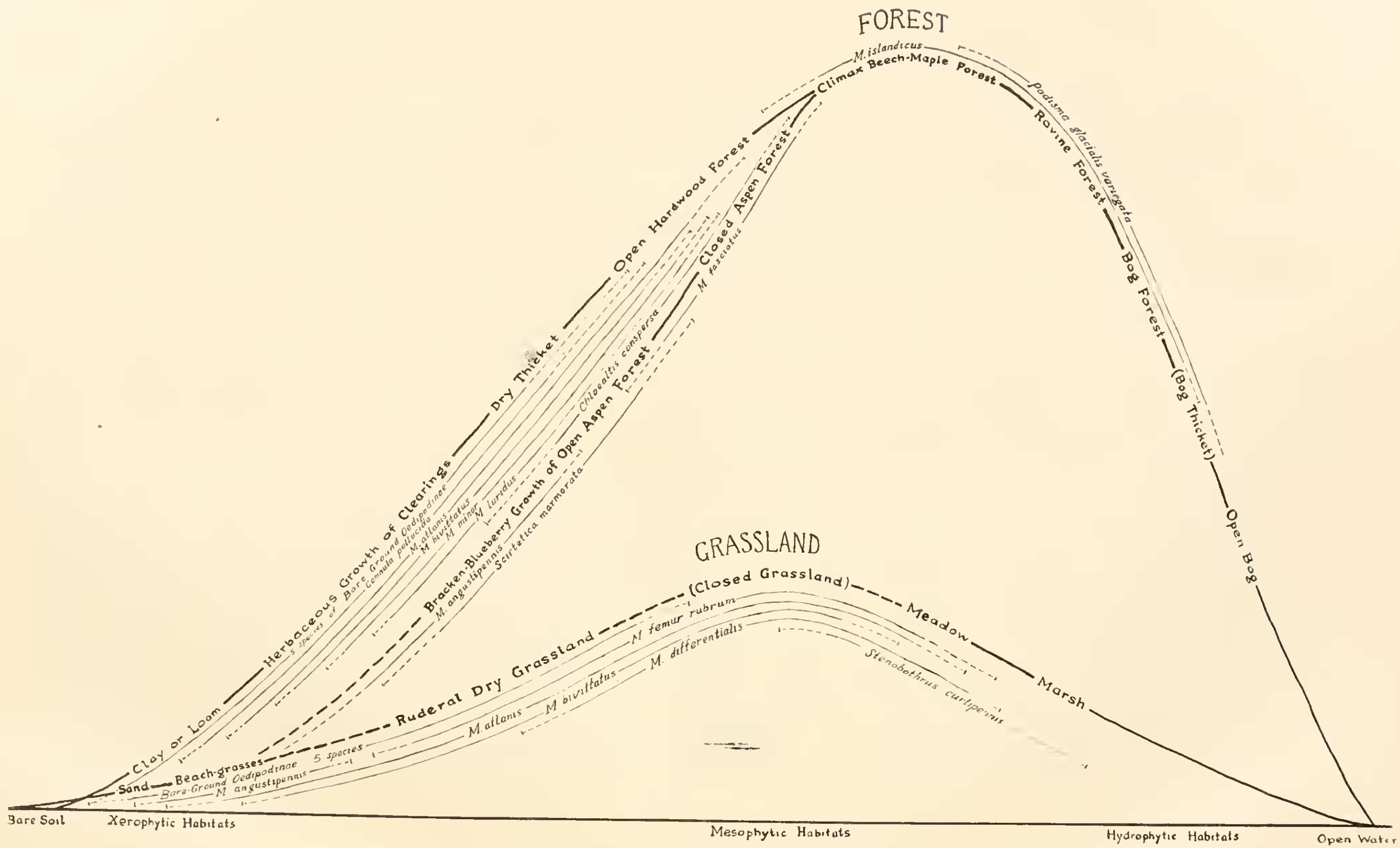
It is further possible to arrange the lines representing the different successional series within a region, so that relations between them may also be seen graphically. Fig. 1 (p. 156) is an arrangement of the gradients of physical and vegetational conditions in the Douglas Lake region, based on the development of vegetation, and accompanied by a representation of the selection of these conditions by the various grasshopper species.

IV. General Discussion.

The Assignment of Terrestrial Animals to Habitats.

It is thought by some zoölogists that the local distribution of most terrestrial animals is more or less haphazard, that there is no order in the distribution of animals into different habitats, or that, if there is order, the conditions of distribution are too complicated to be determined by any present methods. Shelford ('11: 591) points out several reasons for the prevalence of these and similar opinions. On the contrary, environmental relations of animals are now coming to be recognized as quite definite (Shelford, '12*b*: 333).

The habitat, in the sense of abode for animals, is a particular combination of certain environmental conditions, physical and vegetational, and to some extent, animal, uniform over a certain area. More or less variability within this area is the rule, and we may consider the area of the habitat as larger or smaller, according to the degree of uniformity of conditions. In these areas of varying degree, plant and animal communities of various degree find their existence. Ecological classification, aside from its dealings with plant and animal individuals, has to do with the recognition and classification of these degrees of likeness and difference of environments and of plant and animal communities. (See Shelford, '12*b*: 355.) The habitat considered most convenient in the treatment of local distribution of



FOREST
M. islandicus
Climax Beech-Maple Forest
Podisma glacialis variegata
Ravine Forest
Bog Forest
(Bog Thicket)
Open Bog
Open Hardwood Forest
Closed Aspen Forest
M. fasciatus
Dry Thicket
Chloealtis conspersa
Herbaceous Growth of Clearings
5 species of Bare Ground Oedipodinae
Camnula pellucida
M. atlanis
M. bivittatus
M. minor
M. luridus
Bracken-Blueberry Growth of Open Aspen Forest
M. angustipennis
Scirtetica marmorata
Clay or Loam
Sand
Beach-grasses
Bare-Ground Oedipodinae
M. angustipennis
5 species
GRASSLAND
(Closed Grassland)
Meadow
Marsh
Ruderal Dry Grassland
M. femur rubrum
M. differentialis
M. atlanis
M. bivittatus
Stenobothrus curtipennis
Bare Soil
Xerophytic Habitats
Mesophytic Habitats
Hydrophytic Habitats
Open Water

FIG. 1. Showing the relation between grasshopper species and gradients of physical and vegetational conditions within the Douglas Lake region. At the left are initial stages of vegetation developing from dry ground; at the right initial stages developing from wet ground or open water. Conditions vary as development of the vegetation proceeds; at the top of the curve xerophytic and hydrophytic series converge in the climax association. Vegetational control is, roughly, successively greater from bottom to top. Moisture content is successively higher from left to right. Only the initial stages of grassland vegetation would normally be represented in the region, as forest invasion would prevent development of closed grassland. However, certain ruderal associations within the region present conditions essentially those of partially and of nearly closed grassland, and these associations are accordingly placed in the proper place in the gradient of grassland environmental conditions. Stages not well represented within the region are in parentheses (bog thicket, closed grassland). In certain of the gradients the transition between two stages is not direct, as between beach-grass and open aspen forest. Such indirect transitions are represented by dotted lines. The gradient for development of coniferous forest is not shown; it might be represented by a line parallel to the other dry forest gradients.

Approximate range of the grasshopper species in the various gradients is shown by fine lines, which are dotted in the extremes of the range, in which their occurrence is infrequent and their numbers small. It is seen that certain species occur in equivalent stages of the different kinds of vegetation. Species common to hardwood and aspen forests are placed between the two gradients; those restricted to aspen forest are to the right of the aspen gradient.

grasshoppers within a region is the area marked off by the plant association, in which there is a general and usually recognizable uniformity of vegetation and of physical conditions.

A species is to be assigned to a habitat if its occurrence in that habitat is a matter of regularity. In general, the animal species is seldom confined to a single habitat within a region. The determination of the more typical habitats selected by a particular species involves estimation of relative numbers, and presents certain difficulties, which are discussed below. In a regional study of a group of animals taxonomically related, or of all the animals of the region, there are certain other difficulties which obscure the definiteness of habitat relations.

Variation in Range of Habitats in Different Species.—The range of toleration of environmental conditions varies widely among different species of a taxonomic group, and accordingly we find certain animals restricted to one or several similar habitats, while others range over many and different habitats with apparently little discrimination. *Melanoplus atlanis*, for example, occurs regularly in meadows, in dry open grassland, and in open forest. It is a species which can endure widely varying conditions. Upon examination, it is found that it is very much more numerous in certain habitats than in others, and that there are certain habitats in which it occurs only accidentally or not at all. In the Douglas Lake region, it was never seen in cassandra bogs, in bog or ravine forests, in closed aspen forest, and only infrequently or accidentally in closed hardwood forest. There is, then, a *selection* of habitats, and the local distribution of even the most generally distributed forms is far from indiscriminate.

Habitat-Distribution as Affected by Motility of Animals.—The habitat relations of plants are more evident than those of animals because the plant individuals are non-motile, while animal individuals can move about, and it is not to be supposed that they will necessarily stay within a single area of uniform conditions. They continually stray beyond the limits of conditions necessary for all or part of their activities. Among the grasshoppers, certain are much more motile than others, particularly the long-winged and active *Œdipodinæ*. These grasshoppers at times fly high and to considerable distances, and may be seen to traverse

areas of dry grassland, of marsh, and of forest. However, while at rest, very few will be found on trees, for example, or in deep shade, or in dense herbaceous vegetation. They will usually be seen in open dry vegetation or on bare soil. If found in other conditions, these will usually be not far distant from such open situations. Stray individuals are not common and are usually found singly. It is not surprising that stray individuals should be more frequent among species which are very abundant in the region, as *Camnula pellucida*, and among species of the more extensive habitats. The motility of animals is perhaps commonly overestimated as a factor in width of local distribution. The daily itinerary of an animal is likely to be more circumscribed than is usually thought. In the case of the grasshoppers again, for most species the *ordinary* mode of progression is walking or crawling, rather than jumping or flying. Usually grasshoppers are noticed only when disturbed, or "flushed." Their behavior, jumping or flying *when disturbed*, is a special reaction to an approaching object. The ordinary activities are much less frequently observed. Birds, our most motile animals, have very definite habitat relations (see Gates, '11). Though the actual number of observed occurrences of stray individuals in unusual situations may be large, these occurrences are very infrequent and exceptional when compared with occurrences in the normal habitat.

Differences of Activity in Different Habitats.—Various activities of the animal may take place in different strata of one habitat, or in different habitats, separated horizontally. The stratum or habitat of greatest importance to the animal is the one in which the most narrowly limited activity takes place, and this activity is usually concerned with breeding (Shelford, '07, '11).[1] In the case of the Douglas Lake grasshoppers, eggs are laid just below the surface of the soil, or at least in the ground stratum, and proper conditions for oviposition are among the most important considerations which determine the presence of the particular species in the region, and *the* important consideration in determining which habitat within the region is most essential to the

[1] On p. 595 (Shelford, '11) are given references to other authors, in which instances of breeding activities as being most narrowly limited are given for birds and for fishes.

species. The habitats in which few or no grasshoppers are found are those in which the soil is not suitable for egg-laying.

In many animals the breeding period occupies a rather small part of the season of activity, and the adult animal may spend but a small proportion of its active life in the breeding stratum or habitat. The habitat in which the species occurs most regularly and in the greatest numbers is the habitat in which the species is of greatest influence. It is the most important habitat of the species so far as plants and other animals are concerned. In associational studies, in which emphasis is laid upon relations between organisms, this habitat is most important. The animal may feed in several habitats, but principally in the habitat in which it is most frequent and abundant. The feeding activities, though of secondary importance (usually) in determining the presence of an animal in a particular habitat and a particular region, are of primary importance in relation to the communities of plants and animals of which the species becomes a member. In the study of all the habitats within a given region, emphasis would be placed on the habitat in which the species is most frequent and most abundant. The success of the species in the various habitats, as indicated by relative numbers, is a measure of the degree of correspondence between the environmental conditions actually furnished within the area of the habitat, and those required by the animal. The habitat in which the species is found most regularly and in the greatest numbers is the habitat in that region which most closely approximates the optimum environment for the species.

The Different Activities in Climatic and in Local Habitats.—It so happens, in probably the majority of the grasshopper species of the Douglas Lake region, that the feeding habitats and the breeding habitats coincide more or less perfectly. In insects of incomplete metamorphosis, as *Orthoptera*, the possibility for the immature animals to correspond in mode of life rather closely to the adults is much greater than in insects in which changes from larva to adult are more radical. Grasshopper nymphs feed and hop about as do the adults. They cannot fly, but as flying more commonly does not take the animal into another habitat, this difference is of minor importance. Where the

habitat in which the species is more frequent and abundant is of considerable extent within the region, as in climatic associations, soil conditions, or conditions for egg-laying, would be either uniform throughout the area of the habitat, or else suitable small spots would be scattered about within the area. There would then be no necessity for the females to migrate to a different habitat for oviposition. Thus most of the grasshoppers found in the aspen association would be able to lay eggs within its area, and the nymphs would find food and other necessary conditions in the same place as do the adults. In the beech-maple or cedar-bog forests, which individuals of *Melanoplus islandicus* probably rarely leave, suitable egg-laying sites, in this case wood as found in stumps or logs, are scattered about over the forest floor. It thus appears probable, in the extensive habitats provided in terrestrial climatic plant associations, that the correspondence between the conditions required for breeding and the conditions required for feeding and other ordinary activities, may be quite general. Conditions for egg-laying among insects, for example, may still be more restricted than conditions required for other activities, but the local variability of environmental conditions within the area of the plant association is sufficiently wide, usually, to include the more restricted conditions necessary for egg-laying, or whatever the most narrowly limited activity happens to be. If what is true in the case of grasshoppers is true in a large number of terrestrial animals, as seems likely, this means that the limits of the climatic plant association need not be passed, ordinarily, by a large number of the animal species, since all the necessary conditions are supplied within its area. The animal community of the area may be thus, in large measure, self-contained, and coextensive with the plant community.

In local habitats, on the other hand, which are usually restricted in extent and consequently likely to present less variability of environmental conditions within the area, it is less likely that all the conditions necessary for the animal species will be supplied within the area. The number of animal species which can find all the necessary conditions for existence within the area will be comparatively small; thus many of the species will be obliged to perform certain of their activities in other habitats.

Furthermore, environmental conditions in local habitats are likely to be the extreme, rather than the mean, conditions within the region. Thus sedge marsh habitats in the Douglas Lake region have submerged or very wet soil; in the latter case, the growth may be so dense as to leave no exposed soil. These are extreme conditions for terrestrial habitats. The only grasshopper of the region which was seen in such situations is the ectophytic *Stenobothrus curtipennis*. It is probable that this species deposits its eggs in higher and drier soil. Unlike most of the grasshoppers, its ordinary activities can be carried on in a very humid environment, and the presence of exposed soil is not necessary. The conditions necessary for breeding, however, do not correspond with the extreme condition of wet soil, and must be obtained outside the area of the extreme habitat. The local habitat is less likely to be self-contained than the extensive or climatic habitat.

Difficulties Arising from Habitat Complications.—The habitat relations of animals sometimes are much less evident at the tension zone between two contiguous habitats, and there is the further complication that habitats are sometimes distinguished with difficulty. Boundaries will be invaded by animals of both habitats. The tension zone is much wider, and the confusion greater, between two rather similar habitats. As Shull points out ('11: 221), the determination of habitat relations is difficult in regions where the habitats are small in area and much intermingled. The tension zone presents one great advantage in that it allows determination of which species of one habitat range farthest and most frequently into the adjoining habitat. A graded series of species can be determined, which expresses the resultant of different factors entering into habitat selection of the different species.

Unstable habitats are frequently indicated by the presence of mixed plant associations. These contain representatives from two or more plant communities. Thus near the beach of Douglas Lake, the bracken-blueberry growth is mixed with bearberry and juniper heaths, a few small clumps of beach-grasses, in certain spots, and in others by local growths of ruderal bluegrass. In such mixed areas the animal assemblage is not of the constant character seen in more uniform growths.

Mixed conditions within the area of a habitat also tend to confuse. This is particularly well shown in open forest. *Melanoplus fasciatus* and *Chloealtis conspersa*, of the species studied, are found in open forest with a number of other grasshoppers, but appear to be the only two for which forest conditions are really necessary. All the others are grassland species, and are present because of the grassland environment of the ground stratum. Grassland species may be found in very small sunlit grassy patches within a closed forest. These sunlit patches are not to be considered as part of the closed forest habitat. Probably very few insects of the ground stratum are really typical of open forest.

Roadsides and other local modifications are a source of error in assigning animals to a habitat. A collector traveling along the sandy roads through the bracken-blueberry growth of the aspen forest would see large numbers of bare-ground *Œdipodinæ*, almost all on the roads. He might never realize that these grasshoppers are not particularly common in the undisturbed growth, and that they are animals of the roads and not of the bracken-blueberry growth.

Furthermore, the habitat is not entirely uniform within its area. There are many extremely local environmental differences within the habitat, which influence the animal species as well as the plant species. Thus in scattered parts of the bracken-blueberry growth, occasional patches of lichen-covered surface are found. With these patches is associated the grasshopper *Scirtetica marmorata*. It does not occur over the entire bracken-blueberry growth, as does *Melanoplus angustipennis*, for instance.

Within the habitat there are local differences in the degree of development of the vegetation. This is shown in grassland in the degree of openness of vegetation. Where considerable bare surface is exposed between the plants, bare-soil animals are found. In closed grassland, no animals of this habit occur. Differences of development are shown in the aspen forest. Among scattered trees the bracken-blueberry growth presents an environment essentially that of grassland. In more compact tree growths ground conditions begin to approach those of the forest floor. Only in such situations is the short-winged grasshopper *Melanoplus fasciatus* to be found.

Estimation of Relative Numbers in Different Habitats.

The Distinction Between Frequency and Abundance.—Many collectors do not distinguish between frequency of occurrence and abundance of individuals. To them a species is common if scattered individuals are seen frequently, or if numerous individuals are seen infrequently. Frequency refers to regularity of occurrence in one or more habitats; abundance is concerned with numbers of individuals per unit of area. The distinction is indispensable if we are to estimate numbers of individuals in different habitats. Thus many of the conspicuous *Œdipodinæ*, a number of which can be seen in flight at one time, but over a considerable extent, as far as one can see, are frequent species, but are not numerous as compared with certain inconspicuous *Melanopli*, a larger number of which may be found in any area within the habitat as large as a few meters square. These last are abundant *and* frequent.

Difficulties in the Way of Numerical Estimation.—The writer is not acquainted with any very practicable method of estimating absolute numbers of insects in different habitats of a region. Absolute numbers of plants may be estimated under favorable circumstances, as may also the numbers of the larger or more sedentary animals. Following are some of the difficulties encountered in estimating absolute numbers of terrestrial animals: In any one species, there are differences in numbers of individuals, in degree and kind of activity, in readiness with which it is perceived, in ease with which it is captured, or recognized if it is not taken, in time and in space. These conditions vary with the year, with the season, with weather conditions, and with the time of day; they vary in different habitats, in different strata, with different kinds of soil and against different backgrounds, and in different kinds of vegetation. There are many difficulties in the way of estimating even relative numbers of different species. Less abundant species are likely to be confused with more abundant kinds. There are differences in appearance, in conspicuousness, in degree of activity, in ordinary behavior and behavior upon being disturbed, with different species, which make some of these much more readily perceived, or recognized, or captured, than others. Differences in time of appearance and activity, and

in place, in surroundings, may make certain species appear more or less abundant or frequent than they really are.

The method used by Shull ('11: 218) in estimating numbers of grasshoppers per unit of area is valuable, but does not distinguish the different species. His suggestion "to collect immense numbers, and depend upon majorities to decide the usual habitat," besides being impracticable, is not satisfactory, for the numbers collected are not a true index of the numbers which actually occur by reason of the difficulties mentioned above.

The Method Used in Determining Frequency and Abundance.— The method used by the writer was to visit the various habitats, taking one or several grasshopper specimens of each species for verification, and to estimate abundance not from the numbers collected, but from the numbers observed per unit of area in each station, having in mind the considerations which tend to over- or underestimation of actual numbers.[1] If in the bracken-blueberry growth, a considerable number of *Melanoplus angustipennis* could be seen nearby, within a rod or two, and if this condition was practically uniform over the area of the association, as nearly as could be seen, an infinity sign was put down in the field notes opposite its name, indicating numbers in which it occurred, followed by the number collected, thus (∞, 2). If in twenty minutes walk through the aspens only four or five specimens of *Scirtetica marmorata* were seen, and two collected, the notes would appear thus (*s*, 2), the letter *s* representing *several.* If in a half-mile of sandy roadway, a considerable number of specimens of *Spharagemon* were seen, but never close enough together to be abundant, the numbers would be indicated by the plus sign (+, 1). If a species was taken in a particular kind of habitat in nearly all stations of this habitat visited, or if it was regularly

[1] Facilities for determination were available at the biological station, and the species were identified as they were taken. With most of the species the writer had been acquainted, and the species soon became so familiar as to be recognizable at sight. In life there are many rather conspicuous peculiarities of color and of behavior which aid in recognition. Whenever there was doubt as to identity, as in the case of *Melanopli* particularly, specimens were caught and examined critically in the field, to avoid overlooking species of similar appearance. In all cases one or several specimens of each species were kept for verification. There is no reason why many familiar insects should not be recognized at sight as easily as birds are identified by ornithologists.

to be found in extensive areas representing this habitat, its frequency for that habitat was considered to be high. From the records which thus accumulated it was possible to arrive at a relative estimate of frequency and abundance for each species in its various habitats. Though the method is not free from error, it is the best which was available, and it is believed to be not far from a representation of actual conditions. Terms expressing degrees of frequency and abundance are *dominant*, *abundant*, *frequent*, *occasional*, *infrequent*, and *accidental*. These terms are used in the table of distribution on p. 153, and are there defined.

The Relation of the Animal to Plant and Animal Communities.

The Plant Association as an Index of the Habitat.—The area of the habitat as considered in this study has already been defined as the area conveniently marked by the extent of the plant association. In the plant association or plant community physical conditions and vegetation are generally uniform. In the early stages of development of vegetation, local physical conditions dominate. In later stages the vegetation assumes the type determined by climatic conditions, and exerts nearly complete control over local physical factors. Thus the grasshoppers in early stages of vegetation, as the *Œdipodinæ*, most of which live in very open grassland, are more intimately associated with physical conditions, which to them are more important, while those of advanced stages of vegetation depend more upon vegetational factors, and less upon the character of the soil. *Melanoplus islandicus*, associated with climax deciduous forest, is a species of the second type. The grasshoppers as a group are most abundant in early stages of vegetation in forest climates, while in grassland climates they occur abundantly in all stages. The plant association may thus be taken as the index of environmental conditions; it expresses the resultant of physical and vegetational conditions to which animals are subjected. Within the area of the plant association local variabilities in physical conditions are usually accompanied by local variabilities in the vegetation; the latter may exist independently. Grasshopper species are affected by these local differences.

Vertical Distribution.—The distribution of terrestrial animals in space is both vertical and horizontal (Shelford, '12*b*). Most of the grasshoppers of the Douglas Lake region belong to the ground and field (herbaceous) strata, as do the *Acridiidæ* in general. With the exception of the forest species which oviposit in wood, the eggs are laid in the soil. Most of the species require bare soil, and many of their activities take place directly upon the surface. *Stenobothrus* is more commonly seen upon the plants, and certain species of *Melanoplus* live upon the plants part of the time. *Podisma glacialis variegata* is a shrub-inhabiting species. Grasshoppers are in general typical animals of the ground stratum. Other families of *Orthoptera* are more typical of other strata.

Horizontal Distribution.—Within a region an animal species will select habitats or associations in which conditions of the optimum environment are most closely approximated. The table on p. 153 indicates that no two grasshopper species of the Douglas Lake region select the same set of environmental conditions. Certain of the species are similar in distribution, but none are identical. They replace one another in different habitats, with some overlap, and can be arranged in series according to gradients of environmental factors (Fig. 1, p. 156).

Although a single species may be found in more than one association, it is not equally abundant nor equally regular of occurrence in these associations. Certain of the grasshopper species are typical of only one association, as *Melanoplus fasciatus* in closed aspen forest. *Melanoplus atlanis*, the most generally distributed species, though abundant in five habitats, is most abundant in ruderal grassland, and very typical in such situations. Other grasshoppers are *more* characteristic of the other four associations in which *Melanoplus atlanis* is abundant.

The various habitats in which a particular species may be found happen to be more or less similar in physical and vegetational conditions. Data in the table on p. 153 indicate that those associations in which a grasshopper is found in common may agree only in containing certain or all of the conditions necessary for that species, and that there need be no successional or geographic relationships between the associations, nor is it a matter of concern whether the associations be native or ruderal, extensive or local.

The occurrence of a grasshopper species, or of several species, in two habitats or associations does not mean that these furnish similar environmental complexes for animals. It means simply that certain environmental conditions necessary for these particular species are *included* among the conditions provided by these habitats. Thus in the Douglas Lake region, *Melanoplus islandicus* is found in beech-maple forest and in the cedar-bog forest. These two associations are radically different in many respects, as habitats for animals. The entire range of conditions presented within the area of an association, particularly if it be extensive, is likely to be considerably more inclusive than the range of conditions required by many animal species. Taxonomic groups of animals which are affected more particularly by conditions *differing* in the two habitats, will be represented differently in them. It follows that very little reliance can be placed on comparisons of habitats on the basis of the study of a taxonomic group, such as grasshoppers, except in respect of the particular conditions critical to the species of this group. Comparisons of the entire animal communities of the two habitats would not be subject to this limitation, since nearly all of the environmental conditions within the two habitats would come into consideration.

Within any one association the animal species may be distributed generally throughout its area, as *Melanoplus angustipennis* in the bracken-blueberry growth; in certain instances it may be restricted to a part of the area characterized by a slight environmental difference; or it may occur in scattered parts of the association, characterized by scattered local differences, as *Scirtetica marmorata* in the lichen-covered patches within the bracken-blueberry growth.

The Animal Environment.—In addition to the physical and vegetational influences upon the animal species, that of its animal environment must also be recognized. Direct effects of the animal-environment upon the animal species are probably greater than the indirect effects produced by modification of physical and vegetational environments. Among these latter more general effects of the animal community are the accumulation of organic remains, and particularly the effects of phy-

tophagous animals upon vegetation. It is probable that animal environmental influences are greater than is commonly supposed, but that ordinarily they play a subordinate part as compared with physical and vegetational influences (cf. Shelford, '12*a*: 94).

The grasshopper species is not only affected by the animal environment, but is itself a part of it. So far as the relations of the grasshoppers to the association and with other species is concerned, about all that is known, in general, is that they are among the most important of the plant-eating animals of grassland associations, in which some of them are dominant species; and that they form the principal food supply for a comparatively large number of predaceous and parasitic enemies. It is not known to what extent different grasshopper species compete with one another. Differences in habitat and in time of activity may indicate removal of competition among certain species.

Successional Relations.

The successional relations of the Douglas Lake associations have been discussed by Gates ('13: 48), and a diagram illustrating the successions is included. The work on the grasshoppers has not covered so wide an area, consequently many of Gates' associations are not well represented. Fig. 1, on p. 156, will serve to illustrate successional relations of the associations in which grasshoppers were taken, and the changes in grasshopper species may also be seen, as one plant association is replaced by another. Initial stages in dry soil are shown at the lower left-hand part of the diagram; initial stages in wet habitats at the lower right. The two series converge at the top of the curve, in the climax beech-maple forest. The ordinary course of succession from marsh associations is toward bog forest; from beach grass into pine forest. These successions are not shown in the diagram. The aspen association is the result of secondary succession from pine forest, which is no longer well represented in the immediate region. Grassland associations between beach-grass and wet meadows are represented only by ruderal growths; which have originated mostly by secondary succession. Closed grassland is not represented, for invasion by forest occurs before it can develop.

Only the series leading from bare sand to climax forest through the aspen stages of burnt-over pine lands will be discussed in relation to grasshopper succession. The following table, taken from the distribution table on p. 153, and with the same notation, shows the grasshopper species of the various stages. Accidental and atypical occurrences are not recorded. It should be remembered that the bare soil habitat is never extensive in the region, and that grasshoppers of bare soil depend also upon nearby vegetation.

TABLE II.

	Bare Sand.	Beach-Grass.	Bracken-Blueberry.	Closed Aspens.	Beech-Maple.
Dissosteira carolina	Freq.[1]	Freq.	Occas.		
Spharagemon bolli	Freq.[1]	Occas.	Occas.		
Circotettix verruculatus	Freq.	Occas.	Occas.		
Arphia pseudonietana	Freq.[1]	Infreq.	Infreq.		
Hippiscus tuberculatus	Freq.	Infreq.	Infreq.		
Camnula pellucida	Freq.[1]	Freq.[1]	Freq.[1]		
Melanoplus angustipennis	Occas.	Freq.	Dom.		
Melanoplus luridus			Occas.		
Scirtetica marmorata			Infreq.[2]		
Melanoplus fasciatus			Infreq.	Freq.[1]	
Chloealtis conspersa			?	Infreq.	
Podisma g. variegata					?
Melanoplus islandicus					Freq.
Melanoplus atlanis	Freq.[1]	Abund.	Freq.	?	Infreq.

From examination of the table we see that there is a successive change of species with development of vegetation, and that even when species are not replaced with changes in associations, their numbers are successively increased or decreased.

The succession from bare sand to closed hardwood forest includes two successional series, the development from very open grassland growth to closed grassland, and the development of closed forest from open forest growth. The transition stage is the open aspen forest, in which trees are small and scattered. Ground conditions, dominated by the bracken-blueberry cover, are those of grassland which has not yet reached the closed stage. The change in ground conditions from those of grassland to those of closed forest is radical, as shown by the great difference

[1] Frequently found, usually not in numbers, but in a few places approaching abundance.

[2] More typical of scattered patches of lichen-covered surface; distribution in bracken-blueberry not continuous.

between the grasshoppers of the bracken-blueberry and closed aspen stages. Climax beech-maple conditions have probably not yet been fully developed, in the immediate region, from the closed aspens of the pine lands. The beech-maple forest of the morainic areas of the region represent the ultimate condition of present closed aspen areas.

The grasshoppers of the table show certain likenesses and differences in habitat-selection which may be correlated with their behavior characters. The first five species, all typical of very open situations, are active, motile forms, of strong and sustained flight, and are usually seen resting upon bare soil. They lay eggs usually in soil of loose texture. They are frequently seen on roads, and patches of bare soil, in the Douglas Lake region, and are abundant near the beach. They are frequently seen in the interstices between plants in open grassland, and become successively less numerous with the closing of the vegetation.

Camnula pellucida is less like the typical bare-ground *Œdipodinæ* in behavior. It is more variable in distribution, and though practically restricted to grassland, is more numerous in ruderal growths.

Melanoplus angustipennis is an interstitial species, and increases in abundance with the closing of the vegetation until the sand is relatively stable, with the admixture of a little humus, though the soil is still loose in texture.

Melanoplus luridus and *Scirtetica marmorata* have not been found in sufficient numbers to determine their status with satisfaction. The former appears to be a species of nearly closed grassland; the latter is more or less closely associated, in this region at least, with lichen surfaces that had not developed in earlier stages of herbaceous growth.

Melanoplus fasciatus and *Chloealtis conspersa*, in this and other regions, are associated with dry open forests and forest borders. They are more frequently short-winged, and exhibit a departure from grassland behavior. The latter is known to deposit eggs in wood.

Melanoplus islandicus is a shade-dwelling species of deep woods. It is flightless, and probably lays eggs in wood. *Podisma*

glacialis variegata has not been taken in the beech-maple forest, but probably occurs there. It differs from the other grasshoppers of the region in being of the shrub stratum, rather than of the ground or herbaceous strata.

The species in the table are arranged approximately in the order of succession of the associations in which they occur. *Melanoplus atlanis*, being more generally distributed, can hardly be assigned to a particular place in the series, and is placed at the bottom accordingly. It is most abundant in ruderal grassland, and is not at all common in forest.

A parallel development of vegetation in sand is seen in a region in central Illinois. The herbaceous vegetation is sand prairie, is very open in the initial stages, and is replaced by xerophytic oak forest before a closed grassland is reached. The habitat-relations of the various grasshopper species are discussed by Hart ('07). A number of the species of the Douglas Lake region are here represented in habitats occupying equivalent stages in the successional series.

The initial stages of herbaceous growth, characterized by a large proportion of bare surface, are accompanied by active, very motile grasshoppers which rest normally on the surface and which lay eggs in soil of loose texture. With the closing of the herbaceous growth grasshoppers of this habit gradually decrease in numbers, giving way to species which rest part of the time upon the vegetation, which are less motile, and which lay eggs in the less sterile types of soil of such situations. In sand regions of the forest climate, usually, forest invasion occurs before the herbaceous growth becomes closed. The ground conditions remain those of grassland until the forest approaches the closed stage, when the grasshoppers of open grassland are abruptly replaced by forest grasshoppers, which are less motile, usually flightless. They are fewer in species and individuals than grassland members of the group, in part because of the fact that in advanced forest stages, in which the ground is almost entirely covered with dead leaves, the soil is generally inaccessible for egg-laying, and oviposition takes place typically in wood.

Geographic Relations.

The vegetation of the region, as has already been mentioned, is composed of two geographic elements, that of the Northeastern Conifer Province and that of the Eastern Deciduous Province. In addition there are certain associations, chiefly made up of plants which cannot be assigned to these vegetation regions. Comparison was made of the geographic distribution of grasshoppers with that of the vegetation, and with their own local distribution.

Most of the species are generally northern in distribution. Of these *Podisma glacialis variegata*, *Melanoplus islandicus*, and *Chloealtis conspersa* may be assigned to the Northeastern Province. *Circotettix verruculatus*, *Melanoplus fasciatus*, *M. luridus*, *M. minor*, *Camnula pellucida*, and *Stenobothrus curtipennis* range in both northeastern and northwestern coniferous regions, extending south to varying distances in both Appalachian and Rocky Mountains. *Arphia pseudonietana* does not range so far to the east as these preceding species. *Arphia*, *Melanoplus luridus*, *M. minor*, *Camnula*, and *Stenobothrus* occur also throughout the northern part of the Prairie Province.

Spharagemon bolli and *Scirtetica marmorata* may be assigned to the Eastern Deciduous Province. *Hippiscus tuberculatus* is found in the northern parts of both prairie and deciduous forest. *Melanoplus angustipennis* is a prairie species, being found abundantly in sandy parts of the Prairie Province, ranging also west into the sage-brush country, in Utah.

Dissosteira carolina, *Melanoplus atlanis*, *M. femur-rubrum*, *M. differentialis*, and *M. bivittatus* are of very wide geographic distribution, ranging over most of the United States and much of Canada.

Certain species of the first group are rather sharply restricted to the coniferous forest regions, while others range well into the prairie and deciduous forest regions. *Chloealtis* and *M. fasciatus* range also into deciduous forest. *M. luridus*, *M. minor*, *Camnula* (in the northern prairie states), and *Arphia* range also into the prairie region. An excellent instance of the sometimes sharp boundary between two provinces is shown along the foothills of the eastern Rocky Mountains in Colorado. Here *Chloealtis*,

Circotettix, *M. fasciatus*, and *Camnula* are not found outside of the mountains, while *Arphia*, *M. luridus*, and *M. minor* are found on the plains. *Stenobothrus* bears no particular relation to climatic vegetation regions, as its presence is determined by local conditions of moisture.

The occurrence of *Melanoplus angustipennis* at Douglas Lake, so far from the prairie region, seems at first very unusual. So far as the writer is aware, the species is not recorded from Michigan, though it must occur all along the Lake Michigan shore, and is known from Ontario. Its most necessary environmental condition is sandy soil, and this is well developed along most of the shore-line of the Great Lakes.

The five species of most wide distribution geographically are those which have least definite habitat-preferences within a particular area. The extensive range, and the fact that these particular species are among those most important economically, as destructive to crops, is to be explained in terms of tolerance of widely varying conditions.

The species which are restricted to forest habitats in the Douglas Lake district are restricted geographically to forest provinces. Certain of the species found in grassland or in open forest in the region studied range outside the forest provinces, being thus clearly independent of forest growth, while others appear to be restricted to forested regions, though found in open habitats. It is probable that *Camnula pellucida* and *Circotettix verruculatus* are restricted to the mountain areas of Colorado by radical changes in physical conditions from mountains to plains, rather than by changes in vegetation.

In general, it may be said that grasshopper species associated with the climatic plant association have the same geographic range as this association. This range, when shared by many species, determines the ecological province. Where two similar climatic vegetation regions adjoin, as in the case of northeastern and northwestern conifer regions, the same grasshopper species may range over both, in similar associations. Certain species may also range locally into other provinces, in habitats locally approximating those of their own climatic association. Species associated with local habitats may be restricted to the province,

but more usually range over much wider areas (Shelford, '11: 606). Species of very general local distribution within a restricted area are likely to be very generally and very widely distributed geographically, and are the species which most frequently invade ruderal and cultural growths, and which tend to replace other species with the spread of civilization. Species of closed associations show more evident local and geographic relation to the vegetation than species of open associations, in which *local* physical conditions dominate (cf. Shelford, '12*a*: 89, 90).

Seasonal Relations.

Distribution of animals in space is more or less affected by distribution of animals in time. In dealing with the latter it seems that seasonal relations and life-histories of animals are comparable to habitat relations and habitat-preferences, when dealing with distribution in space.

The growing season is not uniform in physical and vegetational features of the environment. Seasonal changes are conveniently marked by changes in *aspect* of the vegetation. The successive changes in the environment for grasshoppers in the course of a season are somewhat different in forest associations from those in grassland.

A field of study of seven weeks is not long enough to determine seasonal relations of grasshoppers, nor to determine what species of grasshoppers occur in that region. *Chortophaga viridifasciata* (De Geer), an early spring grasshopper almost certainly occurs at Douglas Lake. *Melanoplus scudderi* (Uhler) and *Melanoplus punctulatus* (Uhler) may reasonably be expected to occur within the region. Both are short-winged forest-inhabiting species of late summer and autumn.

The time of adult activity of such species as were found, however, is known; the species may be arranged according to life-history into the following groups:

1. Species which hibernate as nymphs, appearing as adults in spring, remaining active only during early summer, represented by *Hippiscus tuberculatus*.
2. Species which hibernate as eggs, maturing very early in summer or late in spring, becoming scarce or disappearing by about September 1. *Melanoplus minor*, *M. bivittatus* (sometimes persisting in numbers till frost), *M. fasciatus* (this species may more properly belong in the fourth group).

3. Species which mature in spring or early summer, but which remain abundant until frost. *Chlœaltis conspersa, Melanoplus angustipennis, M. atlanis, M. femur-rubrum.* The last two are known to be two-brooded, and *M. angustipennis* probably is also, in parts of its range.
4. Species which mature in early July, remaining active until frosts. This is the common grasshopper life-history. *Stenobothrus curtipennis, Camnula pellucida, Dissosteira carolina, Spharagemon bolli, Scirtetica marmorata, Circotettix verruculatus, Melanoplus islandicus, M. luridus.*
5. Late-maturing species, appearing from late in July to the middle of August, and remaining until frosts. *Arphia pseudonietana, Podisma glacialis variegata, M. differentialis.*

The different timing of the period of activity of the species may be correlated with one or both of two kinds of seasonal difference in environmental influence: (1) Changes in physical and vegetational conditions necessary for the various activities. Conditions of temperature, moisture, vegetation, etc., change so materially with the season as to present very different environments for animals at different times of the year. Grasshoppers of different habitat-preferences may perhaps occupy the same area at different seasons. Life-histories are affected by geographic variation of climatic conditions. The entire complex of behavior characters of the animal is intimately associated with its life-history (Shelford, '12*b*: 334). (2) Seasonal differences in antagonistic influence of other animals, particularly those of similar requirements. These influences among animals which eat the roots of the corn plant and the strawberry plant are discussed by Forbes ('09: 296). Different species of certain insect genera, among them *Arphia* and *Hippiscus*, which are of similar habits and which occur in the same association, sometimes are active during successive parts of the season. One species of a genus may be completely replaced by another in a very short time, the second species continuing abundantly during the remainder of the season (Vestal, '13*b*). This replacement of one insect by another of similar habits is not uncommon among species of one genus, though not confined within genera. The differences in time of appearance among all the grasshopper species within a region, with the result that within some of the associations fewer species occur together at one time, may perhaps be accounted for partly in terms of antagonistic animal influence. The fact that grasshopper species of unique habits, which occupy

certain habitats by themselves, so far as grasshoppers are concerned, have the most common type of life-history, hibernating in the egg stage and active from early July till frosts, suggests that antagonistic influence is not a factor in determining *their* life-histories. Such species are *Stenobothrus curtipennis* in marshy growths, and *Melanoplus islandicus* in deep forests.

It appears that the species with least definite habitat-preferences (*Melanoplus atlanis*, *M. femur-rubrum*, *M. bivittatus*) have also least definite life-histories. They mature early, remain active till frosts, and are sometimes two-brooded. Their wide distribution in time is probably due to the same cause as their wide distribution in space, namely, their lack of responsiveness to slight differences in environmental conditions.

V. Summary.

Distribution of grasshopper species within the region studied bears evident relation to the plant associations. The plant association is the index to environmental conditions, and its extent marks the area of the habitat. In studies of local distribution within a region, all the plant associations, including local and ruderal associations, should be considered, since otherwise certain habitat relations may be overlooked.

As an environmental complex, the plant association is usually more inclusive than the total of conditions required by a particular species, particularly if it is climatic or extensive. Associations may be similar as environments for grasshopper species if they agree merely in including physical and vegetational conditions critical to those species. Grasshoppers select habitats or associations in which favorable conditions are to be found, irrespective of past history, extensiveness, geographic or successional relationships of the vegetation. There is very seldom any direct relation between grasshopper species and species composition of the plant associations, as few grasshoppers are selective feeders.

Most of the grasshopper species are of the ground stratum, and soil conditions are essential. These grasshoppers are typical of open herbaceous associations, characteristic in initial stages of vegetational development in dry ground. Species of open forest

are mostly grassland forms, since ground conditions are essentially the same in both situations. In closed forest and moist herbaceous associations species and individuals are less numerous, are not confined to the ground stratum, and are more intimately associated with vegetational conditions. Grasshopper species can be arranged according to gradients of environmental factors (Fig. 1, p. 156).

Grasshopper succession is incidental to the development of vegetation. The change is not only one of species, but of habits as well.

Grasshopper species have in general the geographic range of the types of associations which include the necessary physical and vegetational conditions. The ranges of many species are in agreement with the areas of vegetation provinces. Species of least definite local distribution are widespread geographically.

Seasonal differences in time of activity of grasshopper species are marked. This is probably partly due to antagonistic influence of other animals. Seasonal and local distribution are interrelated. Species of indefinite local distribution have also least definite time distribution.

University of Colorado,

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